

Valentin Kosev¹
Natalia Georgieva²

Inheritance of main quantitative traits in broad bean (*Vicia faba* L.)

Authors' addresses:

¹ Department of Breeding and Seed Production of Forage Crops, Institute of Forage Crops, Plevan, Bulgaria.

² Department of Technology and Ecology of Forage Crops, Institute of Forage Crops, Plevan, Bulgaria.

Correspondence:

Natalia Georgieva
Department of Technology and Ecology of Forage Crops, Institute of Forage Crops, Plevan, Bulgaria.
Tel.: +359 887 733 701
e-mail imnatalia@abv.bg

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ABSTRACT

The purpose of this study was to analyze the values of some genetic parameters of hybrid populations of *Vicia faba*, which would allow rational selection of desired genotypes in terms of main quantitative traits. The field trial was conducted during the period 2016-2018 at the Institute of Forage Crops (Plevan). Four cultivars (Fb 2481, BGE 002106, BGE 029055, BGE 032012) and their hybrids (Fb 2481 × BGE 002106, BGE 002106 × Fb 2481, BGE 029055 × BGE 032012, BGE 032012 × BGE 029055) were subjects of the study and their quantitative traits were observed in generations F1 and F2. Results showed that the plant height, seeds number and seed weight per plant in all crosses were inherited over dominantly. The alleles of the genes that determined more seeds per plant with an increased weight were dominant. The highest values of hypothetic and true heterosis in F1 were found in cross BGE 029055 × BGE 032012 regarding plant height (82.03%, 81.55%), in Fb 2481 × BGE 002106 – for 1st pod height (49.39%, 40.97%), in BGE 002106 × Fb 2481 – for pods number (36.05%, 32.95) and seed weight (225.47%, 161.36%), and in BGE 032012 × BGE 029055 – for seeds number per plant (117.77%, 96.89%). The coefficients of inheritance in all four crosses had medium to high values for the trait of seed weight per plant. Mass phenotype selection will be more effective if it starts in F4-F5 hybrid generations in the crosses Fb 2481 × BGE 002106 for pods and seeds number, in BGE 032012 × BGE 029055 for seeds number, and in BGE 002106 × Fb 2481 for seed weight per plant.

Key words: hybrids, broad bean, heterosis, quantitative traits, inheritance

Introduction

Broad bean (*Vicia faba* L.) is an important legume crop in many countries in the world. Its seeds are considered as an extremely valuable protein source for animal and human nutrition, as they are characterized by a relatively high content of digestible starches and proteins (Crépon *et al.*, 2010; Gnanasambandam *et al.*, 2012; Abd El-Mageed, 2018). In addition, broad bean belongs to the group of plants determined as nitrogen-fixing plants. Therefore, it contributes to sustainable agricultural production through maintaining and improving soil fertility and playing an important role in crop rotation (Jensen *et al.*, 2010; Alhajj *et al.*, 2019). In recent years, considerable efforts have been directed to increase the yield and some quality parameters in the crop. In this regard, the performances of heterosis, transgression, and coefficient of inheritance provide important information for raising seed yield and other characteristics in broad bean (Hazem *et al.*, 2013).

Combining more useful characteristics and properties in a

new variety is possible only through a correct selection of parental forms and the inclusion in the breeding process of cultivars from different breeding centers. A new cultivar should provide a high yield, but at the same time, to have some stability under different conditions (Ershova & Golova, 2013).

One of the most common ways to create new cultivars is through intra-specific hybridization, which allows a wide variety of different forms to be obtained. Depending on the environmental conditions under which the hybrids develop, their genetically determined traits may have different manifestations, i.e. excess compared to parental forms regarding some traits or vice versa. The success in breeding is determined by the values of the traits in the second generation F2, where, among the maximum number of gene combinations, it is necessary to find valuable recombinations (Boroevich, 1984).

The term heterosis is used to define the breeding value of a hybrid, i.e., the excess of the value of the hybrid trait relative to the parental forms. Hypothetic heterosis shows exceedance above the average of the parents, and true heterosis shows higher values of the hybrid compared to better parental form.

The identification of hybrids (with heterosis in the first generation and transgression in the second generation), which have a significant advantage in quantitative (qualitative) traits over their parents, contributes to the continuation of the breeding process in the right direction (Gulyaev & Malchenko, 1983).

The study aimed to analyze the genetic parameters of four hybrid populations of *Vicia faba* to obtain an overview of the inheritance of their main quantitative traits, which will allow rational selection of desired genotypes.

Materials and Methods

The study was conducted during the period 2016-2018 at the Institute of Forage Crops (Pleven). Four cultivars of broad bean (*Vicia faba* L.) were used as parental forms: Fb 2481 (P₁), BGE 002106 (P₂), BGE 029055 (P₃), BGE 032012 (P₄). The first originated in Portugal and the others – in Spain. The following crossings were made: Fb 2481 × BGE 002106 (H₁), BGE 029055 × BGE 032012 (H₃) and their reciprocals (BGE 002106 × Fb 2481 /H₂/, BGE 032012 × BGE 029055 /H₄/). Seeds of the parental and hybrid populations of the first (F1) and second (F2) generations were sown manually, at 50 cm inter-row spacing and 10 cm intra-row spacing. The randomized block method was used (Barov, 1982), with the size of the experimental plot of 4 m². The values of the quantitative traits were determined: plant height (cm), 1st pod height (cm), number of pods and seeds per plant, and seed weight per plant (g).

For all studied traits were calculated the following parameters: true (HPr) and hypothetical (HPh) heterosis effect in F1 regarding the parental form with a higher value of manifestation of the trait; the indicator of transgression (Tn); the number of genes, in which the parents differ (N); dominance (D); epistasis (E), coefficient of inheritance in a broad sense (H2); coefficient of effectiveness of the selection of genotypes by the phenotypical performance of the trait (Pp) (Sobolev, 1976). The cytoplasmic effect (re) was determined according to Reinhold (2002). The positive value of re (re > 0) means that a greater influence on the expression of the signs is the paternally inherited factors, and the negative one (re < 0) means the influence of maternal cytoplasmic heredity (cytoplasmic effect). All experimental data were statistically processed using the MS Excel (2003) and Statgraphics Plus for Windows Version 2.1 software products.

Results

The current practice of developing new cultivars of plants widely uses the method of artificial sexual hybridization, i.e. the crossing two parental forms, differing from each other in certain quantitative or qualitative characteristics. The success of combinative breeding in self-pollinated crops is largely

dependent on the successful selection of parental components for hybridization. In most of the cross-pollinated crops and some of the self-pollinated ones, the heterosis effect is more pronounced in hybrids obtained from crosses between different parental forms that carry very favorable genetic factors. This fact is essential for the practical use of heterosis hybrids.

The trait of plant height from a breeding point of view is very important to develop cultivars in grain direction. The data in the present study indicated that the hybrids outperformed better parents in terms of this trait (Tables 1 and 2). The hybrids H₃ (BGE 029055 × BGE 032012) and H₁ (Fb 2481 × BGE 002106) exhibited higher hypothetical (82.03% and 75.09%) and true heterosis (81.55% and 62.10%) than their reciprocal crosses.

Table 1. Main quantitative traits of parent forms in the broad bean

Parents	Plant height	1 st pod height	Pods number	Seeds number
P ₁	51.67b	27.00a	7.33a	14.00a
P ₂	44.00a	25.00a	7.00a	16.00a
P ₃	48.25a	23.33a	11.17b	24.13a
P ₄	48.00a	24.83a	7.05a	19.50a

Legend: Mean followed by the same letter(s) did not differ significantly at 5% level:

P₁ – Fb 2481, P₂ – BGE 002106, P₃ – BGE 029055, P₄ – BGE

The formation process in F2 hybrids was determined by the „contrast“ of the parents. The strongest manifestations of depression were in hybrids H₂ (29.65%) and H₃ (26.37%). The difference in plant height between plants of F1 and F2 generation in hybrid H₄ was insignificant, which determines a considerably lower level of depression (1.29%). In the hybrids studied, the trait of plant height was inherited positively overdominant, especially strongly expressed in H₃ and its reciprocal (H₄). The numerical expression of the degree of dominance in F2 showed that dominance played a greater role in the trait inheritance.

The 1st pod height is an important starting point for the selection in the breeding process. This characteristic usually correlates directly with plant height. Long-stemmed varieties and hybrids usually form their 1st pod higher. Concerning the values of this trait, the parent cultivars were very similar, and the differences between them were not statistically significant (Table 1). However, in the hybrids obtained, some diversity was found still in F1, as in most cases the reciprocal hybrid formed the 1st pod lower.

Inheriting 1st pod height was similar to the plant height. In almost all hybrids, the heterosis (hypothetical and true) was positive. An exception was the hybrid H₄, which was characterized by manifestations of negative heterosis (-6.56% and -9.37%). Plants of H₁ were distinguished by the highest

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hypothetical (46.39%) and true heterosis (40.97%), while the hybrids obtained by crossing BGE 029055 (as the maternal form) with BGE 032012 (as a paternal component) had the lowest one (-23.72%). In the hybrids obtained from the last two cultivars, the effect of maternal cytoplasm ($re = -6.93$) was very clearly expressed, not only regarding this trait but also in the number of seeds per plant ($re = -3.13$) (Figure 1).

At larger differences between F1 and F2, negative and positive dominance and overdominance were observed due to the action of dominant genes or epistasis. The inheritance of 1st pod height was overdominant ($hp1 > 1$) in H₁, H₂ and H₃. In H₄, the degree of dominance in F2 (10.07) was considerably higher than F1 (-2.12), indicating that epistatic gene actions were crucial for the trait manifestation.

The way of inheriting the traits that determine plant productivity is a necessary condition for increasing grain yield when applying effective selection in the hybrid material. The traits of the number of pods and seeds per plant and seed weight per plant had the most direct relationship with this indicator.

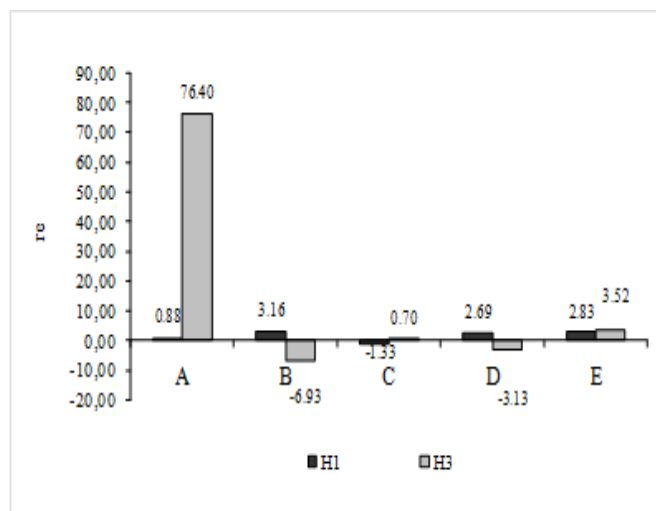


Figure 1. Cytoplasmic effect (re) at inheritance of the studied traits in F1 hybrid generation

A – plant height, B – 1st pod height, C – pods number, D – seeds number, E – seed weight per plant

H₁ – Fb 2481 × BGE 002106, H₃ – BGE 029055 × BGE 032012

Table 2. Heterosis, depression and degree of dominance for quantitative traits in the investigated crosses

Hybrids	F1	F2	Hypothetic heterosis (HPh, %)	True Heterosis (HPr, %)	Depression in F2 (%)	Degree of dominance in F1	Degree of dominance in F2
Plant height							
H ₁	83.75	64.30	75.09	62.10	23.22	9.37	8.59
H ₂	77.00	54.17	60.98	49.03	29.65	7.61	3.30
H ₃	87.60	64.50	82.03	81.55	26.37	315.80	262.00
H ₄	68.50	67.62	42.34	41.97	1.29	163.00	311.87
1 st pod height							
H ₁	38.06	30.45	46.39	40.97	20.00	12.06	8.90
H ₂	31.75	31.50	22.12	17.59	0.79	5.75	11.00
H ₃	32.90	37.25	36.63	32.53	-13.22	11.83	35.32
H ₄	22.50	27.84	-6.56	-9.37	-23.72	-2.12	10.07
Pods number							
H ₁	9.31	9.61	29.94	26.99	-3.19	12.88	29.32
H ₂	9.75	7.33	36.05	32.95	24.79	15.50	2.00
H ₃	12.40	7.25	36.14	11.04	41.53	1.60	-1.81
H ₄	9.50	11.16	4.30	-14.93	-17.46	0.19	1.99
Seeds number							
H ₁	21.00	20.66	40.00	31.25	1.62	6.00	11.32
H ₂	26.38	14.17	75.83	64.84	46.29	11.38	-1.67
H ₃	33.00	10.00	51.29	36.79	69.70	4.84	-10.22
H ₄	47.50	26.38	117.77	96.89	44.47	11.11	3.95
Seed weight							
H ₁	16.50	8.19	86.79	50.00	50.36	3.54	-0.59
H ₂	28.75	7.00	225.47	161.36	75.65	9.19	-1.69
H ₃	34.50	5.00	188.80	150.15	85.51	12.22	-7.53
H ₄	21.50	9.65	79.98	55.89	55.13	5.18	-2.49

Legend: H₁ – Fb 2481 × BGE 002106, H₂ – BGE 002106 × Fb 2481, H₃ – BGE 029055 × BGE 032012, H₄ – BGE 032012 × BGE 029055

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Parent cultivars P₁, P₂ and P₄ (Table 1) were characterized by similar expression of the pods number (7). On the other side, P₃ significantly exceeded the rest, forming an average of 11-12 pods per plant. With the highest average value for this trait was the cross H₃ (12.40). For other crosses, pods number did not exceed 10. Strong positive hypothetical and true heterosis was observed in almost all hybrids. The exception was H₄, in which the hypothetical heterosis was positive but considerably weaker, and the true heterosis was negative (-14.93%).

The strongest manifestation of hypothetical and true heterosis in F₁ regarding the investigated trait was found in H₂ (36.05%; 32.95%). Hybrid H₃ also had a high value of hypothetical heterosis, but at the same time, the plants from this cross were the most depressed (41.53%). On this indicator, there were some differences related to the direction of crossing. When cultivars Fb 2481(P₁) and BGE 032012 (P₄) were in the position of the maternal component, the hybrids did not show signs of depression (-3.19% and -17.46%).

When inheriting pods number in F₁, the tendency was mainly overdominance (except for H₄ where the inheritance was incomplete). Epistatic gene interactions had influence in crosses H₁ and H₄ in F₂.

For the purposes of breeding regarding seeds number per plant, the cross H₄ was of interest. This cross was characterized by intermediate inheritance of the trait in F₁, as in F₂ the importance of dominance prevailed. It is characteristic of the other crosses was the positive dominance (overdominance) in the inheritance of pods number. In the F₂ generation, in H₂ and H₃, the overdominance was determining at inheritance, and in H₁ – epistasis.

As a summary feature for determining crop productivity, the seed weight per plant is used. As a quantitative trait, it is too much influenced by environmental conditions and may vary widely. The analysis of the data showed that concerning seed weight, all hybrids showed strong positive heterosis (hypothetical and true). Stronger manifestations of heterosis were found when crossing BGE 002106 with Fb 2481 (H₂) (225.47%; 161.36%). In the second hybrid combination with the highest values was H₃ (188.80%; 150.15%), and in the reciprocal combination, the heterosis effect was about twice lower (79.98% and 55.89%).

The considered trait was characterized by clear-pronounced positive overdominance in all hybrid combinations, especially in H₃ (12.22). In F₂, for the inheritance of the trait, dominant gene effects had an influence. Considerable manifestations of depression were observed in all hybrid plants, less pronounced in H₁ (50.36%).

The data in Table 3 showed that the number of genes (N) in which hybrid H₄ differed regarding plant height was 103, and at hybrid H₁ – 93. For the remaining traits, the hybrid forms of H₃ were differed essentially in the number of genes,

especially in terms of pods number (928) and 1st pod height (676). When changing the direction of crossing, the effect of maternal cytoplasm of BGE 032012 (P₄) had influence, and therefore the differences in the hybrids were smaller. The number of genes in which H₁ differed (for the number of pods and seeds) was also smaller.

Table 3. Values of gene parameters for the quantitative traits of the investigated crosses in F₂ generation

Hybrids	Tn	N	D	E	H2	Pp
Plant height						
H ₁	-1.42	93	-1.59	13.66	68.40	-1.54
H ₂	-2.68	13	26.19	5.21	8.94	-12.97
H ₃	1.33	31	17.93	9.27	46.69	-9.89
H ₄	1.25	103	41.78	-27.00	72.82	-12.46
1 st pod height						
H ₁	-0.59	98	39.63	-25.61	6.59	-12.04
H ₂	1.80	7	2.05	2.26	18.72	-0.55
H ₃	0.97	676	198.88	-158.89	52.21	-56.73
H ₄	1.35	139	27.58	-30.20	11.21	-5.00
Pods number						
H ₁	0.75	21	-2.09	4.90	11.03	0.74
H ₂	0.24	51	18.78	-13.49	3.62	-4.70
H ₃	-1.98	928	-138.80	181.40	2.43	-22.08
H ₄	-1.87	181	42.91	-40.76	32.37	-9.81
Seeds number						
H ₁	3.20	59	-6.69	11.87	23.40	0.52
H ₂	2.31	29	12.71	-8.13	1.79	-3.12
H ₃	-1.34	349	-59.95	71.43	16.27	-8.47
H ₄	3.56	28	-1.27	5.64	22.96	0.19
Seed weight						
H ₁	4.19	123	-13.45	23.28	20.02	0.07
H ₂	3.86	52	-6.06	10.59	71.70	0.49
H ₃	0.19	183	-24.75	35.84	37.41	-1.43
H ₄	0.96	47	-6.68	10.09	21.57	0.13

Legend: H₁ – Fb 2481 × BGE 002106, H₂ – BGE 002106 × Fb 2481, H₃ – BGE 029055 × BGE 032012, H₄ – BGE 032012 × BGE 029055

Tn – transgression (Tn); N – number of genes, in which the parents differ; D – dominance; E – epistasis; H2 – coefficient of inheritance in broad sense; Pp – coefficient of effectiveness of the selection of genotypes by phenotypical performance of the trait

From the indicator of transgression (Tn), it is evident that at the crossing of P₁ with P₂, homozygous genotypes with gene recombinations leading to a substantial increase in plant height can hardly be expected. This is slightly more likely to occur when crossing P₃ with P₄, where the numerical expression of the parameter was slightly positive. Transgressive forms can be obtained at the cross H₁ and its reciprocal (H₂), concerning

the seeds number (3.20; 2.31) and seed weight per plant (4.19; 3.86). When crossing P₄ (as a maternal component) with P₃ (as the paternal component), genotypes with more and heavier seeds per plant can also be obtained.

From the values of allele interactions, it was established overdominance of the dominant alleles determining the expression of 1st pod height (39.63; 2.05; 198.88; 27.58). Interactions of a similar nature were found in H₂ for plant height (26.19), pods number (18.78) and seeds number (12.71) per plant, as well as in H₄ for plant height (41.78) and pods number (42.91).

With regard to the indicator of interallele interactions, it can be noted that for most of the studied traits, epistasis was negative for some of the hybrids. This suggests that their phenotypic manifestation will decrease compared to their full phenotypic inheritance. Positive epistasis interactions were found in all four crosses for seed weight per plant (23.28; 10.59; 35.84; 10.09). Exceptions were crosses H₄ (for plant height, -27.00) and H₂ (for seeds number per plant, -8.13).

Inheritance is a characteristic of the relative share of genetic differences and differences caused by the environment in the phenotypic variability. Under a change of genotype or environmental conditions, it is necessary to change the assessment of inheritance. The coefficients of inheritance for all four crosses showed a relatively higher share in the phenotypic manifestation of the main trait (seed weight per plant), with values of 20.02, 71.70, 37.41 and 21.57%.

The number of seeds and pods are traits that are highly influenced by changes in the growing environment. The low value of their inheritance coefficients implies leading an effective selection for desirable traits in later hybrid generations (F₄-F₅) when the effects of dominance and epistasis diminish and homozygosity increases. For these traits, a medium to high inheritance was established in cross H₄ (32.37%; 22.96%). With relatively high inheritance was the plant height in H₄ (72.82%) and H₁ (68.40%), as well as the 1st pod height in H₃ (52.21%).

The coefficients of effectiveness of the selection indicated that the probability of mass selection of suitable genotypes by phenotype in early hybrid generations (F₃-F₄) was quite low for most of the traits. Success in the breeding program for obtaining new forms of broad beans with increased numbers of pods and seeds can be achieved by conducting a selection in the offspring of H₁ (regarding the number of pods /0.74/ and seeds /0.52/), H₄ (for seeds number /0.19/) and H₂ (for seed weight per plant /0.49/).

Discussion

According to Link *et al.* (2008), the objectives of broad bean breeding entirely depend on the economic and agro-ecological conditions, and the geographical area and use.

Classical breeding has made marked progress in terms of nonshattering, yield stability and increased yield, highly improved lodging resistance. Still, progress in breeding is complicated by the partial alagomy of the crop.

Many authors reported various manifestations of heterosis effects of economic traits and desirable heterosis values over those of the better parent for characteristics such as earliness and yield components in *V. faba* (Alghamdi, 2009; Ibrahim, 2010). Link *et al.* (2008) found considerable heterosis in the first generation, as F₁ hybrids outperformed their parents in most cases by more than 40%. In support of this, Zeid *et al.* (2004) and Ibrahim (2010) established yield heterosis in which F₁ hybrids provide yield more than both the mid-parent mean and the higher-productive parent. Heterosis was also recorded in F₂, with a yield of F₂ approximately at the mid-point of the F₁ hybrid and the parent mean, as theoretically expected.

Other researchers (Gasim & Wolfgang, 2007) reported significant inbreeding depression in terms of plant height and seed productivity in broad bean hybrids, which is considered as strong evidence of heterosis manifestations in these characteristics. This was in line with the results of the present study. However, according to Bishnoi *et al.* (2012), inbred depression in the second hybrid generation (F₂) was not always associated with heterosis in F₁. These data were confirmed by the results of Ceyhan (2003), who found nonadditive gene interactions and manifestations of overdominance for the number of pods per plant.

According to Schill *et al.* (1998), inter-pool crosses provide greater heterosis than intra-pool crosses. Diversity in the breeding program can be introduced by backcrossing between elite lines as recurrent parents and external germplasm in a pre-breeding strategy. The selected lines can then be evaluated for potential as components of a synthetic variety.

When studying of inheritance of the first pod height of soybean hybrids, Kostylev & Vershinin (2010) observed a different type of inheritance (from complete dominance to the absence of one). Different inheritance has also been observed in some of the reciprocal crosses, which the authors explain with the influence of cytoplasmic hereditary factors. Concerning the degree of inheritance of quantitative traits in the broad bean, Toker (2009) stated that the coefficient of inheritance in a broad sense for grain yield and its components varied over a very wide range (8.80-70.90%), especially for the number of pods and weight per 100 seeds. The same author considered that by using these two traits can successfully increase grain yield.

Bhardwaj & Vikram (2004) considered that when dominant gene actions prevail in the traits related to productivity, breeding in early hybrid generations is unlikely to lead to rapid success.

Conclusion

The analysis of the inheritance of quantitative traits in four hybrid populations (Fb 2481 × BGE 002106, BGE 002106 × Fb 2481, BGE 029055 × BGE 032012 and BGE 032012 × BGE 029055) of *Vicia faba* showed some important dependencies.

The traits of plant height, seeds number and seed weight per plant in all crossings were inherited over-dominantly. The alleles of the genes that determined more seeds per plant with an increased weight were dominant. The highest values of hypothetical and true heterosis in F1 were found in cross BGE 029055 × BGE 032012 regarding plant height (82.03%, 81.55%), in Fb 2481 × BGE 002106 – for 1st pod height (49.39%, 40.97%), in BGE 002106 × Fb 2481 – for pods number (36.05%, 32.95) and seed weight (225.47%, 161.36%), and in BGE 032012 × BGE 029055 – for seeds number per plant (117.77%, 96.89%). The prevailing negative epistatic interactions at some of the crosses (BGE 032012 × BGE 029055 – for 3rd plant height, 1st pod height, pods number and BGE 002106 × Fb 2481 – for pods number and seeds number), suggest a decrease in the degree of phenotypic manifestation of these traits compared to their additive inheritance. The coefficients of inheritance in all four crosses had medium to high values for the trait of seed weight per plant (20.02, 71.70%, 37.41%, 21.57%). Mass phenotype selection will be more effective if it starts in F4-F5 hybrid generations in the crosses Fb 2481 × BGE 002106 for pods number (0.74) and seeds number (0.52), in BGE 032012 × BGE 029055 for seeds number (0.19) and in BGE 002106 × Fb 2481 for seed weight per plant (0.49).

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